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Abstract

Living organisms establish complex networks of mutualistic and antagonistic interactions in nature, which impact strongly on their own survival and on the stability of the whole population. Fungi, in particular, can shape natural as well as man-managed ecosystems due to their ubiquitous occurrence and the range of interactions they establish with plants, animals and other microbes. This review describes some examples of mutualistic and antagonistic fungal interactions that are of particular interest for their ecological role, or because they can be exploited by man to improve plant health and/or productivity in sustainable agriculture and forestry.

Keywords

Biocontrol fungi, fungal interactions, mycorrhizal fungi

Fungi are extremely diversified and versatile organisms that are important players in both natural and man-managed ecosystems. In addition to their main role as decomposers, fungi can establish numerous interactions with other organisms; some of these interactions may be beneficial for all partners involved (mutualistic interactions), whereas others are detrimental for at least one partner (antagonistic interactions). The interactions can be dynamic at both ecological and evolutionary time scales, and shift along a natural continuum from mutualism to antagonism, depending on shifting cost/benefit ratios (Kiers & Denison 2008). Here, we describe some examples of mutualistic and antagonistic fungal interactions that are of particular interest for their ecological role in nature, or because they can be exploited by man to improve plant health and/or productivity in sustainable agriculture and forestry.

Mutualistic interactions: The mycorrhizal symbioses

Genetic and functional fungal diversity in mycorrhizal symbioses

Mycorrhiza is one of the most ubiquitous associations involving fungi, established with the roots of most terrestrial plants. The main function of mycorrhizal fungi is to improve plant mineral nutrient acquisition in exchange for plant photosynthates. However, mycorrhizal fungi may perform many other significant roles, including protection of the plant from biotic and abiotic stress. Mycorrhizal types have been distinguished primarily on the basis of structural characteristics of the symbiotic interfaces and the taxonomic identity of the symbionts (Smith & Read 2008). Mycorrhizal plants generally associate with multiple fungal partners, often playing different functions in the symbiosis (Feddermann et al. 2010). Molecular methods have been instrumental in revealing/identifying fungi in symbiotic tissues and in the evaluation of genetic and functional fungal diversity.

Although the association is generally mutualistic, with bilateral nutrient exchange, host responses may range from positive to negative. Conversely, exploitation of the fungal partner by the host plant without any apparent benefit in return also occurs. Some of these features are described below for specific mycorrhizal types.

Ectomycorrhiza (ECM) is characteristic of trees and shrubs (Figure 1(a) and 1(b)). In this symbiosis, fungal hyphae remain extracellular and increase the surface contact area with root cells, thus improving plant nutrition (Bonfante & Anca 2009). This relationship (mostly with Basidiomycetes) is a prerequisite for the development of the extraradical mycelium and the fruiting bodies. The study of ECM fungal diversity has initially focused on the screening and the molecular identification of fruiting bodies and, only subsequently, of ectomycorrhizal tips (Horton & Bruns 2001). As each ECM species is specialized in exploiting specific resources of the soil ecosystem, investigations have focused on the spatial distribution of the extraradical mycelium. Hebeloma cylindrosporum was the first ECM fungus to be detected in soil (Guidot et al. 2002), and Zampieri et al. (2010) have recently identified, in a truffle ground, a new haplotype of Tuber melanosporum never described from fruiting bodies. Thus, soil is a source of genetic variability as yet unknown. Since individuals within a species vary in functional attributes, such as nutrient utilization, the next step towards a better understanding of how biodiversity drives ecosystem functioning will need to consider the intraspecific diversity of mycorrhizal plants and fungi (Johnson et al. 2012). Current technologies such as pyrosequencing are accelerating research by facilitating complete genome sequencing (Shendure & Ji 2008). The genomes of some ECM species (Laccaria bicolor and T. melanosporum) have already been sequenced (Martin et al. 2008a, 2010) but many others are on their way. As more genomes within the same species will be sequenced, their comparison (population genomics) will facilitate the identification of conserved traits, as well as of different adaptations to the environment.

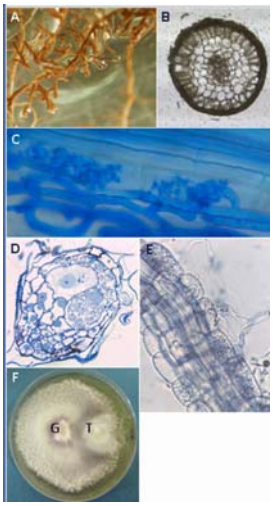

Figure 1: Some examples of fungal interactions. (A)–(E): Mycorrhizal interactions – (A) ECM formed by T. melanosporum on Corylus avellana; (B) – the same ECM in cross section (courtesy of Raffaella Balestrini); (C) – light microscopy of an Oryza sativa root colonized by a field AM fungus forming arbuscules; (D) – cross section of a developing orchid seed colonized by a field ORM fungus (courtesy of Michele Rodda); (E) – root of Calluna vulgaris colonized by field ERM fungi; (F), antagonistic interaction between mycelia of G. fujikuroi (G) and endophytic T. saturnisporum (T) in dual culture.

The symbiotic fungi that form arbuscular mycorrhiza (AM) are among the most important soil organisms. During root colonization, AM fungi develop intracellular arbuscules (Figure 1(c)) that represent the key structures of a functional symbiosis (Balestrini et al. 2011). Ribosomal gene sequences have placed AM fungi in the phylum Glomeromycota, a sister clade to Ascomycota and Basidiomycota (Schüβler et al. 2001), and different genomic loci/genes are continuously being sequenced to further support the definition of this phylum and to clarify evolutionary patterns within the group (Corradi et al. 2004; van der Heijden et al. 2004; Lee & Young 2009; Kruger et al. 2012). Glomeromycota were considered a species-poor group, with about 300 species, but new genera have been recently identified or renamed, as Rhizophagus, Funelliformis, Ambispora, Pacispora, Kuklospora, Otospora and Diversispora (Oehl et al. 2011; Kruger et al. 2012). AM fungi are thought to be the oldest group of organisms living in symbiosis with land plants (Redecker et al. 2000). They colonize the roots of most land plants, where they facilitate mineral nutrient uptake from the soil in exchange for plant-assimilated carbon (Smith & Read 2008). AM fungi are obligate biotrophs, and although their spores can germinate in the absence of host plants, they depend on a living photoautotrophic partner to produce the next generation of spores. Genome sequencing of representative AM fungi, such as Glomus intraradices (DAOM 197198) (synonymous Rhizophagus irregularis; www.amf-phylogeny.com), is currently in progress, but due to the obligate biotrophic status of the fungus, it has encountered unexpected difficulties (Martin et al. 2008b). While waiting for a completely annotated and assembled genome, the increasing number of EST sequences and transcriptomic analyses, obtained inside the Glomus Genome Consortium, have provided new clues to understand the biology of these fungi (Tisserant et al. 2012).

In the last decade, investigations on the functional role of AM fungi in ecosystems indicated that AM fungal communities with different taxon compositions may induce different growth responses in plants, both in laboratory (van der Heijden et al. 1998) and in natural conditions (Moora et al. 2004). Thus, AM fungi may influence the structure and composition of vascular plant communities (Klironomos 2003). The recent use of new metabarcoding approaches based on high-throughput sequencing is providing detailed information on the AM fungal assemblages (Öpik et al. 2009; Lumini et al. 2010; Dumbrell et al. 2011; Becklin et al. 2012; Lin et al. 2012), thus increasing our understanding on the diversity of AM fungal communities in natural and agricultural soils.

The Orchidaceae is one of the most species-rich angiosperm families, including about one-tenth of all flowering plants, with estimates of more than 25,000 species (Royal Botanic Gardens, Kew 2009). Orchids grow from extremely small seeds nearly devoid of nutritional reserves (Rasmussen 1995; Kull & Arditti 2002), and the establishment of a relationship with mycorrhizal fungi is required for seed germination and early development (Figure 1(d)).

Molecular PCR-based techniques (Taylor & McCormick 2008) have facilitated the identification of fungal partners of orchid mycorrhiza (ORM), especially those recalcitrant to isolation in axenic culture or characterized by a paucity of distinctive and stable morphological features. Molecular studies have shown that most fungi involved in most fungi involved in ORM are basidiomycetes (Taylor et al. 2002; Shefferson et al. 2005; Girlanda et al. 2006, 2011; Suárez et al. 2006; Pecoraro et al. 2012b; Dearnaley et al. 2012), but some orchid species form symbioses with ascomycetes (Bidartondo et al. 2004; Selosse et al. 2004; Shefferson et al. 2008).

ORM is quite peculiar because early physiological studies, starting from Smith (1967), have shown that carbohydrates move from the mycobionts to the developing orchid plant; this trophic strategy whereby orchid seedlings are entirely nutritionally dependent upon fungi is called myco-heterotrophy (Leake 1994). Demonstration of carbon transport from orchid to fungus is more controversial (Alexander & Hadley 1985; Smith & Read 2008), and only recently a bidirectional transfer of carbon between the green-leaved terrestrial orchid Goodyera repens (L.) R. Br. and its fungal symbiont was documented (Cameron et al. 2006) by carbon and nitrogen stable isotope analyses. This technique is a powerful tool for understanding the orchid–fungus resource exchange both in nature and in artificial microcosms (Gebauer & Meyer 2003).

In adult plants, orchid–fungus relationship evolves following three distinct directions. Whereas most orchids are photosynthetic at the adult stage, more than 200 orchid species remain completely achlorophyllous. For these species, the main, and usually the sole, source of carbon is provided by the fungal symbionts (Bidartondo et al. 2004; Roy et al. 2009). Molecular investigations have revealed that fully myco-heterotrophic orchids usually associate with narrow clades of fungi that form ECM on neighbouring trees (Selosse et al. 2002; Taylor et al. 2002). Obligate myco-heterotrophic orchids that adopt this mycorrhizal strategy are considered as “cheating parasites” because they obtain carbohydrates from the surrounding photoautotrophic plants, via a shared mycorrhizal fungus (see discussion on mycorrhizal networks below). Some achlorophyllous orchid species, such as Gastrodia sesamoides R. Br., associate instead with free-living saprotrophic fungi, such as Coprinus sp. (Martos et al. 2009; Dearnaley & Bougoure 2010).

A third nutritional mode, in which fungi partly subsidize photosynthetic orchids with both organic and inorganic compounds, is termed “partial mycoheterotrophy” or “mixotrophy” (Selosse et al. 2004) and accounts for a significant number of forest species (Julou et al. 2005; Girlanda et al. 2006; Tedersoo et al. 2007). Mixotrophy allows plants to colonize shaded habitat like dense forests and to be more or less independent of irradiance (Preiss et al. 2010). Investigation of fungal diversity in these ORM indicates a wider range of fungi than obligate myco-heterotrophic species, still including mostly ECM species (Bidartondo et al. 2004).

Fully photosynthetic orchids should not depend on their mycorrhizal partners for organic carbon, and are expected to form less specific associations than mixotrophic or myco-heterotrophic orchids. Most fungi isolated from photosynthetic orchids belong to the anamorphic form-genus Rhizoctonia (Otero et al. 2002; Liebel et al. 2010; Girlanda et al. 2011; Jacquemyn et al. 2011a; Pecoraro et al. 2012a). These Rhizoctonia-like orchid symbionts include a variety of teleomorphic taxa, such as Ceratobasidium, Tulasnella and Sebacina, which are rarely observed in nature (Wright et al. 2010; Venturella et al. 2011).

Culture-dependent and culture-independent molecular analyses were used to identify the mycorrhizal fungi associated with four orchid species in meadow environments across Italy (Girlanda et al. 2011). Two of the orchid species, Ophrys fuciflora and Orchis purpurea, exhibited more specific mycobiont communities compared with the other two species, Anacamptis laxiflora and Serapias vomeracea. Stable isotope analysis showed that all orchid species were significantly enriched in fungal-derived nitrogen, thus indicating that they depend on their fungal symbionts for this element. O. purpurea also obtained carbon from fungi. These findings indicate that mycorrhizal specificity is not restricted to fully or partially non-photosynthetic orchids, since photosynthetic species can also associate with specific fungal clades not shared with other sympatric orchids.

Despite our rapidly increasing knowledge on fungal diversity in ORM, several questions remain open on the presence and extension of ORM fungi in soil and on the relationship between below-ground and above-ground abundance. For example, various studies have outlined an underground association of Russulaceae with Corallorhiza maculata (Taylor & Bruns 1999) and Limodorum abortivum (Girlanda et al. 2006). As underground networks can be better understood by integrated analysis above and below ground (Molina et al. 2011), epigeous macromycetes were surveyed in semicircular sample plots of increasing distances from Limodorum populations in central-southern Tuscany (Italy). The presence, above ground, of various ECM species (among them the genus Inocybe was well represented) that were not found in Limodorum roots (i.e. below ground) indicates that the specificity of this orchid for the Russula complex, in particular R. delica and R. chloroides, is the result of active partner selection. Moreover, the presence of R. delica nearby the orchid of carpophores suggests a link between these two partners (Perini et al. 2007).

Ericoid mycorrhizal (ERM) fungi form a distinct endomycorrhiza (Figure 1(e)) with plant genera in the Ericaceae (Perotto et al. 2012). The study of ERM fungi is a good example of how the development of molecular tools to investigate fungal diversity has impacted on our view of the

specificity in this symbiosis. Considered for a long time a highly specific interaction restricted to few taxa of plants and fungi (Straker 1996), ERM symbiosis is now recognized to encompass a diverse assemblage of symbiotic fungi that features culturable ascomycetes in the Helotiales and Onygenales, but also unculturable basidiomycetes in the Sebacinales (Selosse et al. 2007). Fungal symbionts in the Helotiales are mostly grouped in the "R. ericae aggregate", a large clade first identified by Vrålstad et al. (2002) also including sequences of ECM fungi and root endophytes from other host plants. In the Onygenales, only Oidiodendron maius or phylogenetically close species form mycorrhizal associations with Ericaceae in the field (Lacourt et al. 2002).

ERM plants dominate in heathlands characterized by very poor nutrient status and considerable edaphic stress, and their success in these harsh environments is ascribed to the functional traits of their symbiotic fungi (Smith & Read 2008). ERM fungi are in fact able to exploit recalcitrant organic substrates thanks to an arsenal of extracellular enzymes, and they can withstand high concentrations of toxic compounds. Among ERM fungi, the metal-tolerant O. maius strain Zn (Martino et al. 2000) is becoming a model system to investigate functional traits involved in substrate degradation and metal tolerance because of its recently sequenced genome, and because tools are available for genes identification and genetic transformation (Abbà et al. 2009).

Networking abilities of mycorrhizal fungi

One of the most striking advances in mycorrhizal study is the view of it as a network in natura. The idea of a one plant – one fungus association derives from pioneer works that elucidated the impact of mycorrhizal symbiosis on the host plant ex situ. Such simple models are still instrumental in investigating the functioning of the mycorrhizal symbiosis. However, the mycorrhizal symbiosis involves diverse coexisting plants and fungi: an individual Populus tremula tree may harbour hundreds of ECM fungal species (Bahram et al. 2011), and a given fungus may colonize several plants, even from different species, thus forming mycorrhizal networks between coexisting plants. It is now well known that mycorrhizal fungal diversity influences plant diversity and vice versa (van der Heijden et al. 2003), and the mycorrhizal networks likely contribute to this.

Evidence for mycorrhizal networks between different plant species in natural plant communities derives from barcoding of mycorrhizal fungi using the ribosomal DNA (rDNA). In AM, lack of specificity has long been thought to be the rule (Klironomos 2000). Although recent molecular studies of AM fungal diversity has revealed plant preferences for some Glomeromycetes under field conditions (Vandenkoornhuyse et al. 2003), and that some plant ecological traits may be linked to different fungal preferences (Öpik et al. 2009), many fungal symbionts are shared between coexisting plant species. However, our understanding of the level of symbiotic specificity in Glomeromycetes remains limited because "species" delineation is difficult in these asexual fungi.

In ECM fungi, genets often extend over metres (Douhan et al. 2011) and thus can colonize the roots of multiple hosts to form ECM networks. Although the fine-scale assignment of a single ECM

fungal genet to different co-occurring plants is still preliminary (Selosse et al. 2002; Saari et al. 2005), populations of the model species Laccaria amethystina growing under different host trees were not differentiated when investigated by microsatellites (Roy et al. 2008), indicating that true generalist ECM fungal species do exist.

On the basis of ITS barcoding, earlier reports suggested that multihost fungi dominate forest ecosystems (>90% of the ECM fungal community, see e.g. Cullings et al. 2000); however, later studies revealed more rare ECM fungi and suggested that less than 50% of fungal species were multihost (e.g. Richard et al. 2005). Strikingly, the most common fungi are often shared between hosts (Richard et al. 2005; Diédhiou et al. 2010), while apparent specialization is often linked to rare species: this raises the possibility that the later observation is an artefact due to rarity. Phylogenetic relatedness may be an important parameter in the level of networking, as multihost fungi were an exception in studies involving phylogenetically distant tree species (Smith et al. 2009). Another interesting finding is that the different mycorrhizal types may not form isolated networks, as demonstrated for some fungi taking part in two types of interactions (e.g. ericoid or orchid mycorrhizal fungi that belong to ECM species, as stated above); in addition, several plant species have both ECM and AM partners, such as several Pinaceae and Salicaeae.

Functional aspects of mycorrhizal networks have been thoroughly reviewed (Selosse et al. 2006; Simard et al. 2012): case studies reveal that these networks allow exchange of water, phosphorous and nitrogen between plants. In some plant lineages, even carbon can be received through mycorrhizal networks, as described for myco-heterotrophic and mixotrophic plants (Gebauer & Meyer 2003; Tedersoo et al. 2007). Mycorrhizal networks may be thus involved in plant–plant facilitation or antagonism. For example, they may act to support some forest seedlings growing in the shade (Diédhiou et al. 2010) and there is evidence, at least from simplified systems, for indirect interactions between some AM plant species (van der Heijden et al. 2003). Recently, mycorrhizal networks were suggested to transfer defence-signalling molecules between plants (Song et al. 2010) or allelochemical molecules, resulting in reduced growth of target plants (Barto et al. 2011). More in situ experiments are still needed to assess the relevance and exact contribution, among other mechanisms, of the diverse features of mycorrhizal networks in shaping the plant communities. This is even more complicated by the recent finding that plants can choose to preferentially interact with the most favourable fungi (i.e. the more efficient nutrient providers; Kiers et al. 2011; Selosse & Rousset 2011). As most approaches remain plant centred, the symmetrical impact of the networking between fungi by way of shared host plant species remains to be investigated for the fungus.

Recently, a new level of analysis of mycorrhizal networks has emerged: the bipartite network at species level. The plant–mycorrhizal fungus interaction can be seen as a bipartite network, where species interact with a range of partners that can themselves interact with other species. Here, the links between species on both sides of the plant–fungus interaction are investigated at the whole ecosystem level, as the sum of all observed interactions. These bipartite networks potentially shape co-evolution of the partners, and their architecture has recently attracted much attention in several other biotic interactions (Bascompte & Jordano 2007): mutualistic networks (e.g.

pollinators and plants) tend to be nested, i.e. specialized species associate with a subset of the partners with which non-specialized species associate (Bascompte et al. 2003). Parasitic or predatory networks, in contrast, tend to be modular, i.e. the network is divided into subnetworks within which species preferentially (or exclusively) interact. Not unexpectedly, the AM symbiosis revealed nested networks (Montesinos-Navarro et al. 2012). The same was found for ORM networks (Jacquemyn et al. 2011b; Martos et al. 2012), a particularly interesting result since the mutualistic nature of this symbiosis remains controversial. Further investigations on mycorrhizal networks as bipartite networks are awaited, especially to study responses of the network to disturbance or environmental changes, since they may be crucial parameters for ecosystems resilience.

Antagonistic interactions: Fungi as biocontrol agents

Fungi for biocontrol of plant pathogens and parasites

Biological control exploits antagonistic interactions that exist in nature to reduce the damage caused, mainly to plants, by pathogens and pests. In natural microbiota, certain micro-organisms are in fact able to suppress growth of other micro-organisms through competition for nutrients and/or through the production of inhibitory substances. Numerous examples of fungal antagonism have been described for biocontrol of fungal plant pathogens, nematodes, weeds and insects (Barron 2004; Vega et al. 2009; Güerri-Agulló et al. 2011). Some examples of biocontrol by fungi are discussed here.

Biocontrol of Fusarium head blight (FHB). FHB is one of the most devastating diseases of wheat (Triticum aestivum) worldwide, causing significant reduction of grain yield and quality (Parry et al. 1995; Windels 2000). The disease is caused by a complex of species belonging mostly to the Fusarium genus and including F. graminearum and F. culmorum (Xu & Nicholson 2009). The most serious consequence of FHB is the contamination of grain and cereal products with Fusarium mycotoxins (Peraica et al. 1999), such as the trichothecenes deoxynivalenol (DON) and its acetylated derivates. Early detection and control of trichothecene-producing Fusarium spp. is crucial to prevent toxins entering the food chain. Biological control is a promising strategy and could also be used as part of an integrated management of the disease. Several efforts have been made to identify biological antagonists, which could be used in biological or integrated pest management strategies. Most of FHB species life cycle is saprotrophic and depends on retaining occupation of colonized plant debris, which serves as inoculum, in competition with other micro-organisms (Xu & Nicholson 2009). Mycobiota of haulms buried in soil, treated and untreated with DON, represents therefore an interesting source of potential antagonists and competitors to be exploited in a multitrophic approach for biocontrol of FHB (Sarrocco et al. 2012a).

Several fungal species have been examined for their ability to reduce the potential inoculum of Fusarium pathogens, mainly by reduction of biomass in plant residues colonized by Fusarium (Dawson et al. 2004; Luongo et al. 2005). Trichoderma spp. aggressively colonize crop residues throughout the decomposition process, and competition seems to be more important than mycoparasitism (Naef et al. 2006). Within the Trichoderma genus, an isolate of Trichoderma

gamsii was recently selected for its ability to grow in the presence of DON, for its antagonistic abilities against F. culmorum and F. graminearum mycotoxigenic strains, also on natural substrates (Matarese et al. 2012), and for its capacity to inhibit DON production by both pathogens.

Field experiments confirm the promising biocontrol effect of this T. gamsii isolate, alone and in combination with a Pythium sp. isolate deriving from other investigation (Sarrocco et al. 2012a). The addition of antagonists in soil, alone or in combination, strongly reduced the FHB index of up to about 50%. When applied during anthesis, the most critical phase in wheat life cycle for Fusarium infection, T. gamsii alone caused a significant reduction of the disease index and disease severity, with a reduction of about 85% of the FHB index (Sarrocco et al. in press).

In conclusion, both Trichoderma and Pythium isolates act as competitors of crop residues in soil, a scenario of great importance during the saprotrophic phase of F. graminearum and F. culmorum life cycle, and open the possibility to use these antagonistic strains, also in combination with other organisms, to develop a multitrophic approach in the biocontrol of FHB (Sarrocco et al. 2011).

Biocontrol of the fungal pathogen Gibberella fujikuroi. The decline of the cosmopolitan common reed, Phragmites australis (Cav.) Trin. ex Steudel (Poaceae) has been observed in many European countries, and primarily ascribed to the die-back syndrome (van der Putten 1997). Few investigations in Italian ecosystems have been conducted on reed die-back, one on the brackish waters of Sacca di Goro, in the Po delta in Northern Italy (Fogli et al. 2002), and the other on the large freshwater ecosystem of Lake Trasimeno in Central Italy (Gigante et al. 2011). Several biotic and abiotic factors have been implicated in P. australis decline, the biotic factors including endophytic toxin producing plant pathogens such as G. fujikuroi (Sawada) Wollenw (Angelini et al. 2012; Ostendorp 1989).

To identify a suitable strategy for biological control of G. fujikuroi and to ensure protection of the delicate ecological balance of P. australis, recent studies (Angelini & Venanzoni in press) have isolated endophytic fungi found in declining reed tissues and tested their antagonistic activity against G. fujikuroi (isolate 34) in vitro. Some of these fungal isolates could inhibit G. fujikuroi mycelial growth in dual cultures: Trichoderma saturnisporum Hammill had the maximum inhibitory effect on G. fujikuroi mycelial growth 30 days after inoculation, with a reduction of almost 60% compared to the control, whereas isolates of Acremonium sp., Penicillium concentricum Samson, Stolk & Hadlok and Pycnidiophora dispersa Clum showed significantly modest mycelial growth inhibition, with reductions in the range of 5.1–16.5%.

In dual cultures with G. fujikuroi, antagonistic T. saturnisporum showed initial deadlock 10 days after inoculation (Figure 1(f)) followed by complete replacement of G. fujikuroi.

These results demonstrate the potential role of fungal endophytes to prevent or reduce damage caused by G. fujikuroi to reed plants. The mechanisms of action are currently unknown and may include competition for nutrients and space, production of inhibitors and allelochemicals, or induction of the plant systemic response (Bailey et al. 2008). Due to its greater capacity to inhibit

G. fujikuroi mycelial growth and its higher antagonism index, T. saturnisporum is a good candidate for further studies, testing additional isolates from different geographic origins and sources.

Biocontrol of the insect pest Rhynchophorus ferrugineus. The globalization of markets and insufficient phytosanitary controls of mature palms were the main causes of the introduction in Italy of the red palm weevil (RPW) R. ferrugineus (Olivier) (Coleoptera, Curculionidae). The rapid spread of this pest in various areas of the Mediterranean Basin (Longo & Colazza 2008) has started in the early 1990s (Barranco et al. 1996). According to Barranco et al. (2000), this weevil affects more than 20 palm species, and is currently considered to be the most damaging insect pest of palms in the world.

Despite the great potential of insect biocontrol by entomopathogenic fungi, witnessed by ca. 7000 papers on related topics since 1983 (Vega et al. 2009), there is still limited success in the control of RPW. Fungi that kill insects are a very diverse group, with 700 estimated species in approximately 90 genera (Vega et al. 2009). Among them, most anamorphic fungi, such as Beauveria bassiana (Bals.) Vuillemin and Metarhizium anisopliae (Metschn.) Sorokin, are facultative pathogens that can live as saprobes in soil and are important regulators of insect populations under natural conditions.

Studies on RPW in Sicily have found abundant mycelium at different stages of the insect life cycle (Torta et al. 2008), and fungal isolation has revealed the occurrence of many fungal taxa, including B. bassiana and Metarhizium sp., that was isolated only from adults.

Preliminary bioassays to test the efficacy of a B. bassiana strain isolated from naturally infected RPW larvae, as well as of a commercial formulation based on M. anisopliae and B. bassiana (Vitale et al. 2008), showed that treatments with B. bassiana lead to 90% mortality of the treated larvae, but only 25% of adults. Treatment with the commercial formulation significantly reduced the number of adults and larvae, compared to the untreated controls. These results confirm that selection of entomopathogenic isolates is an important step for successful biocontrol of RPW. Gindin et al. (2006) examined the susceptibility of RPW to M. anisopliae and B. bassiana strains, and found the former to be more virulent, with 100% larval mortality within six to seven days. Güerri-Agulló et al. (2011) investigated the infection process of R. ferrugineus by B. bassiana and developed a solid mycoinsecticide based on B. bassiana. Their results indicate that B. bassiana could be a significant component of a sustainable integrated pest management programme for RPW in Mediterranean areas.

In conclusion, the diverse range of research themes described here show how fungi – through their interactions with other organisms such as plants, animals and microbes – contribute with essential functions to both natural and agroecosystems. Better understanding of the genetic and functional diversity of these fungi will provide us with deeper knowledge of the complexity of mutualistic and antagonistic mycobiomes, and with interesting isolates for biotechnological applications.

References

1. Abbà, S, Khouja, HR, Martino, E, Archer, DB and Perotto, S. 2009. SOD1-targeted gene disruption in the ericoid mycorrhizal fungus Oidiodendron maius reduces conidiation and the capacity for mycorrhization. Mol Plant Microbe, 22: 1412–1421.

2. Alexander, C and Hadley, G. 1985. Carbon movement between host and mycorrhizal endophyte during the development of the orchid Goodyera repens Br. New Phytol, 101: 657–665.

3. Angelini, P, Rubini, A, Gigante, D, Pagiotti, R, Reale, L and Venanzoni, R. 2012. The endophytic fungal communities associated with the leaves and roots of the common reed (Phragmites australis) in Lake Trasimeno (Perugia, Italy) in declining and healthy stands. Fungal Ecol, 5: 683–693.

4. Angelini, P and Venanzoni, R. in press. Antagonistic activity of endophytic fungi towards Gibberella fujikuroi assessed by in vitro tests. Afr J Microbiol Res,

5. Bahram, M, Põlme, S, Kõljalg, U and Tedersoo, L. 2011. A single European aspen (Populus tremula) tree individual may potentially harbour dozens of Cenococcum geophilum ITS genotypes and hundreds of species of ectomycorrhizal fungi. FEMS Microbiol Ecol, 75: 313–320.

6. Bailey, BA, Bae, H, Strem, MD, Crozier, J, Thomas, SESamuels, GJ. 2008. Antibiosis, mycoparasitism, and colonization success for endophytic Trichoderma isolates with biological control potential in Theobroma cacao. Biol Control, 46: 24–35.

7. Balestrini, R, Bianciotto, V and Bonfante, P. 2011. “Mycorrhizae”. In Handbook of soil sciences: Properties and processes, 2nd ed., Edited by: Huang, PM, Li, Y and Sumner, ME. 29–39. Boca Raton, FL: CRC Press.

8. Barranco, P, de la Peňa, JA, Martín, MM and Cabello, T. 2000. Rango de hospedantes de Rhynchophorus ferrugineus (Olivier, 1790) y diámetro de la palmera hospedante (Coleoptera, Curculionidae). Bol San Veg Plagas, 26: 73–78.

9. Barranco, P, de la Peña, J and Cabello, T. 1996. El picudo de las palmeras, Rhynchophorus ferrugineus (Olivier), nueva plaga en Europa. Phytoma, 67: 36–40.

10. Barron, G. 2004. “Fungal parasites and predators of rotifers, nematodes, and other invertebrates”. In Biodiversity of fungi: Inventory and monitoring methods, Edited by: Mueller, GM, Bills, GF and Foster, MS. 435–450. New York: Elsevier Academic Press.

11. Barto, EK, Hilker, M, Muller, F, Mohney, BK, Weidenhamer, JD and Rillig, MC. 2011. The fungal fast land: Common mycorrhizal networks extend bioactive zones of allelochemicals in soils. PLoS ONE, 6: e27195

12. Bascompte, J and Jordano, P. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. Annu Rev Ecol Evol S, 38: 567–593.

13. Bascompte, J, Jordano, P, Melian, CJ and Olesen, JM. 2003. The nested assembly of plant-animal mutualistic networks. P Natl Acad Sci USA, 100: 9383–9387.

14. Becklin, KM, Hertweck, KL and Jumpponen, A. 2012. Host identity impacts rhizosphere fungal communities associated with three alpine plant species. Microbial Ecol, 63: 682–693.

15. Bidartondo, MI, Burghardt, B, Gebauer, G, Bruns, TD and Read, DJ. 2004. Changing partners in the dark: Isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. P R Soc London B, 271: 1799–1806.

16. Bonfante, P and Anca, IA. 2009. Plants, mycorrhizal fungi, and bacteria: A network of interactions. Annu Rev Microbiol, 63: 363–383.

17. Cameron, DD, Leake, JR and Read, DJ. 2006. Mutualistic mycorrhiza in orchids: Evidence from plant-fungus carbon and nitrogen transfers in the green-leaved terrestrial orchid Goodyera repens. New Phytol, 171: 405–416.

18. Corradi, N, Hijri, M, Fumagalli, L and Sanders, IR. 2004. Arbuscular mycorrhizal fungi (Glomeromycota) harbour ancient fungal tubulin genes that resemble those of the chytrids (Chytridiomycota). Fungal Genet Biol, 41: 1037–1045.

19. Cullings, KW, Vogler, DR, Parker, VT and Finley, SK. 2000. Ectomycorrhizal specificity in a mixed Pinus contorta and Picea engelmannii forest in Yellowstone National Park. Appl Environ Microbiol, 66: 4988–4991.

20. Dawson, WAJM, Jestoi, M, Rizzo, A, Nicholson, P and Bateman, GL. 2004. Field evaluation of fungal competitors of Fusarium culmorum and F. graminearum, causal agents of ear blight of winter wheat, for control of mycotoxin production in grain. Biocontrol Sci Technol, 14: 783–799.

21. Dearnaley, JDW and Bougoure, JJ. 2010. Isotopic and molecular evidence for saprotrophic Marasmiaceae mycobionts in rhizomes of Gastrodia sesamoides. Fungal Ecol, 3: 288–294.

22. Dearnaley, JDW, Martos, F and Selosse, M-A. 2012. “Orchid mycorrhizas: Molecular ecology, physiology, evolution and conservation aspects”. In Springer Heidelberg: The Mycota IX, Edited by: Hock, B. 207–230. Fungal associations.

23. Diédhiou, AG, Selosse, M-A, Galiana, A, Diabaté, M, Dreyfus, BBâ, AM. 2010. Multi-host ectomycorrhizal fungi are predominant in a Guinean tropical rainforest and shared between canopy trees and seedlings. Environ Microbiol, 2: 2219–2232.

24. Douhan, GW, Vincenot, L and Selosse, M-A. 2011. Population genetics of ectomycorrhizal fungi: From current knowledge to emerging directions. Fungal Biol, 115: 569–597.

25. Dumbrell, AJ, Ashton, PD, Aziz, N, Feng, G, Nelson, MDytham, C. 2011. Distinct seasonal assemblages of arbuscular mycorrhizal fungi revealed by massively parallel pyrosequencing. New Phytol, 190: 794–804.

26. Feddermann, N, Finlay, R, Boller, T and Elfstran, M. 2010. Functional diversity in arbuscular mycorrhiza: The role of gene expression, phosphorous nutrition and symbiotic efficiency. Fungal Ecol, 3: 1–8.

27. Fogli, S, Marchesini, R and Gerdol, R. 2002. Reed (Phragmites australis) decline in a brackish wetland in Italy. Mar Environ Res, 53: 465–479.

28. Gebauer, G and Meyer, M. 2003. 15N and 13C natural abundance of autotrophic and mycoheterotrophic orchids provides insight into nitrogen and carbon gain from fungal association. New Phytol, 160: 209–223.

29. Gigante, D, Venanzoni, R and Zuccarello, V. 2011. Reed die-back in southern Europe? A case study from Central Italy. CR Biol, 334: 327–336.

30. Gindin, G, Levski, S, Glazer, I and Soroker, V. 2006. Evaluation of the entomopathogenic fungi Metarhizium anisopliae and Beauveria bassiana against the red palm weevil Rhynchophorus ferrugineus. Phytoparasitica, 34: 370–379.

31. Girlanda, M, Segreto, R, Cafasso, D, Liebel, HT, Rodda, MErcole, E. 2011. Photosynthetic Mediterranean meadow orchids feature partial mycoheterotrophy and specific mycorrhizal associations. Am J Bot, 98: 1148–1163.

32. Girlanda, M, Selosse, M-A, Cafasso, D, Brilli, F, Delfine, SFabbian, R. 2006. Inefficient photosynthesis in the Mediterranean orchid Limodorum abortivum is mirrored by specific association to ectomycorrhizal Russulaceae. Mol Ecol, 15: 491–504.

33. Güerri-Agulló, B, Lopez-Follana, R, Asensio, L, Barranco, P and Lopez-Llorca, LV. 2011. Use of a solid formulation of Beauveria bassiana for biocontrolof the red palm weevil (Rhynchophorus ferrugineus) (Coleoptera: Dryophthoridae) under field condition in SE Spain. Fla Entomol, 94: 737–747.

34. Guidot, A, Debaud, JC and Marmeisse, R. 2002. Spatial distribution of the below-ground mycelia of an ectomycorrhizal fungus inferred from specific quantification of its DNA in soil samples. FEMS Microbiol Ecol, 42: 477–486.

35. Horton, TR and Bruns, TD. 2001. The molecular revolution in ectomycorrhizal ecology: Peeking into the black-box. Mol Ecol, 10: 1855–1871.

36. Jacquemyn, H, Brys, R, Cammue, BPA, Honnay, O and Lievens, B. 2011a. Mycorrhizal associations and reproductive isolation in three closely related Orchis species. Ann Bot, 107: 347–356.

37. Jacquemyn, H, Merckx, V, Brys, R, Tyteca, D, Cammue, BPAHonnay, O. 2011b. Analysis of network architecture reveals phylogenetic constraints on mycorrhizal specificity in the genus Orchis (Orchidaceae). New Phytol, 192: 518–528.

38. Johnson, D, Martin, F, Cairney, JWG and Anderson, JC. 2012. The importance of individuals: Intraspecific diversity of mycorrhizal plants and fungi in ecosystems. New Phytol, 194: 614–628.

39. Julou, T, Burghardt, B, Gebauer, G, Berveiller, D, Damesin, C and Selosse, M-A. 2005. Mixotrophy in Orchids: Insights from a comparative study of green individuals and nonphotosynthetic individuals of Cephalantera damasonium. New Phytol, 166: 639–653.

40. Kiers, ET and Denison, RF. 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. Annu Rev Ecol Evol S, 39: 215–236.

41. Kiers, ET, Duhamel, M, Beesetty, Y, Mensah, JA, Franken, OVerbruggen, E. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science, 33: 880–882.

42. Klironomos, JN. 2000. “Host-specificity and functional diversity among arbuscular mycorrhizal fungi”. In Microbial biosystems: New frontiers, Edited by: Bell, CR. 845–851. Halifax, Canada: Atlantic Canada Society for Microbial Ecology.

43. Klironomos, JN. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology, 84: 2292–2301.

44. Kruger, M, Kruger, C, Walker, C, Stockinger, H and Schußler, A. 2012. Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level. New Phytol, 193: 970–984.

45. Kull, T and Arditti, J. 2002. Orchid biology: Reviews and perspectives, VIII, Dordrecht: Kluwer.

46. Lacourt, I, Girlanda, M, Perotto, S, Del Pero, M, Zuccon, D and Luppi, AM. 2002. Nuclear ribosomal sequence analysis of Oidiodendron: Towards a redefinition of ecologically relevant species. New Phytol, 149: 565–576.

47. Leake, JR. 1994. The biology of mycoheterotrophic (‘saprophytic’) plants. Tansley Review No. 69. New Phytol, 127: 171–216.

48. Lee, J and Young, JPW. 2009. The mitochondrial genome sequence of the arbuscular mycorrhizal fungus Glomus intraradices isolate 494 and implications for the phylogenetic placement of Glomus. New Phytol, 183: 200–211.

49. Liebel, HT, Bidartondo, MI, Preiss, K, Segreto, R, Stöckel, MRodda, M. 2010. C and N stable isotope signatures reveal constraints to nutritional modes in orchids from the Mediterranean and Macaronesia. Am J Bot, 97: 903–912.

50. Lin, X, Feng, Y, Zhang, H, Chen, R, Wang, JZhang, J. 2012. Long-term balanced fertilization decreases arbuscular mycorrhizal fungal diversity in an arable soil in north china revealed by 454 pyrosequencing. Environ Sci Technol, 46: 5764–5771.

51. Longo, S and Colazza, S. 2008. Il Punteruolo Rosso delle palme e il Castnide delle palme. Report – Regione Sicilia, Assessorato Agricoltura e Foreste Progetti FITOPALMINTRO- MEDEA, 1: 7–11.

52. Lumini, E, Orgiazzi, A, Borriello, R, Bonfante, P and Bianciotto, V. 2010. Disclosing arbuscular mycorrhizal fungal biodiversity in soil through a land-use gradient using a pyrosequencing approach. Environ Microbiol, 12: 2165–2179.

53. Luongo, L, Galli, M, Corazza, L, Meekes, E, de Haas, Lvan der Plas, CL. 2005. Potential of fungal antagonists for biocontrol of Fusarium spp. in wheat and maize through competition in crop debris. Biocontrol Sci Technol, 15: 229–242.

54. Martin, F, Aerts, A, Ahrén, D, Brun, A, Danchin, EGDuchaussoy, F. 2008a. The genome of Laccaria bicolor provides insights into mycorrhizal symbiosis. Nature, 452: 88–92.

55. Martin, F, Gianinazzi-Pearson, V, Hijri, M, Lammers, P, Requena, NSanders, IR. 2008b. The long hard road to a completed Glomus intraradices genome. New Phytol, 180: 747–750.

56. Martin, F, Kohler, A, Murat, C, Balestrini, R, Coutinho, PMJaillon, O. 2010. Périgord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis. Nature, 464: 1033–1038.

57. Martino, E, Turnau, K, Girlanda, M, Bonfante, P and Perotto, S. 2000. Ericoid mycorrhizal fungi from heavy metal polluted soils: their identification and growth in the presence of zinc ions. Mycol Res, 104: 338–344.

58. Martos, F, Dulormne, M, Pailler, T, Bonfante, P, Faccio, AFournel, J. 2009. Independent recruitment of saprotrophic fungi as mycorrhizal partners by tropical achlorophyllous orchids. New Phytol, 184: 668–681.

59. Martos, F, Munoz, F, Pailler, T, Kottke, I, Gonneau, C and Selosse, M-A. 2012. The role of epiphytism in architecture and evolutionary constraint within mycorrhizal networks of tropical orchids. Mol Ecol, 21: 5098–5109.

60. Matarese, F, Sarrocco, S, Gruber, S, Seidl-Seiboth, V and Vannacci, G. 2012. Biocontrol of Fusarium head blight: Interactions between Trichoderma and mycotoxigenic Fusarium. Microbiology, 158: 98–106.

61. Molina, R, Horton, T, Trappe, J and Marcot, B. 2011. Addressing uncertainity: How to conserve and manage rare or little known fungi. Fungal Ecol, 4: 134–146.

62. Montesinos-Navarro, A, Segarra-Moragues, JG, Valiente-Banuet, A and Verdú, M. 2012. The network structure of plant-arbuscular mycorrhizal fungi. New Phytol, 194: 536–554.

63. Moora, M, Öpik, M, Sen, R and Zobel, M. 2004. Native arbuscular mycorrhizal fungal communities differentially influence the seedling performance of rare and common Pulsatilla species. Funct Ecol, 18: 554–562.

64. Naef, A, Senatore, M and Défago, G. 2006. A microsatellite based method for quantification of fungi in decomposing plant material elucidates the role of Fusarium graminearum DON production in the saprophytic competition with Trichoderma atroviride in maize tissue microcosms. FEMS Microbiol Ecol, 55: 211–220.

65. Oehl, F, Sieverding, E, Palenzuela, J, Inechen, K and da Silva, GA. 2011. Advances in Glomeromycota taxonomy and classification. IMA Fungus, 2: 191–199.

66. Öpik, M, Metsis, M, Daniell, TJ, Zobel, M and Moora, M. 2009. Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. New Phytol, 184: 424–437.

67. Ostendorp, W. 1989. 'Die-back' of reeds in Europe: A critical review of literature. Aquat Bot, 35: 5–26.

68. Otero, JT, Ackerman, JD and Bayman, P. 2002. Diversity and host specificity of endophytic Rhizoctonia-like fungi from tropical orchids. Am J Bot, 89: 1852–1858.

69. Parry, DW, Jenkinson, P and McLeod, L. 1995. Fusarium head blight (scab) in small grain cereals – A review. Plant Pathol, 44: 207–238.

70. Pecoraro, L, Girlanda, M, Kull, T, Perini, C and Perotto, S. 2012a. Molecular identification of root fungal associates in Orchis pauciflora Tenore. Plant Biosyst, 146: 985–991.

71. Pecoraro, L, Girlanda, M, Kull, T, Perini, C and Perotto, S. 2012b. Analysis of fungal diversity in Orchis tridentata Scopoli. Cent Eur J Biol, 7: 850–857.

72. Peraica, M, Radic, B, Lucic, A and Pavlovic, M. 1999. Toxic effects of mycotoxins in humans. Bull World Health Organ, 77: 754–766.

73. Perini C, Salerni E, Pecoraro L, Leonardi P, de Dominicis V. 2007. Hotspot orchids and the fungal community above ground, XV Congress of European Mycologists, 16?21 September 2007, Saint Petersburg, p. 228

74. Perotto, S, Martino, E, Abbà, S and Vallino, M. 2012. "Genetic diversity and functional aspects of ericoid mycorrhizal fungi". In The Mycota IX, Edited by: Hock, B. 255–286. Springer Heidelberg: Fungal associations.

75. Preiss, K, Adam, IKU and Gebauer, G. 2010. Irradiance governs exploitation of fungi: Fine-tuning of carbon gain by two partially myco-heterotrophic orchids. Proc R Soc London B, 277: 1333–1336.

76. Rasmussen, HN. 1995. Terrestrial orchids: From seed to mycotrophic plant, Cambridge, UK: Cambridge University Press.

77. Redecker, D, Kodner, R and Graham, LE. 2000. Glomalean fungi from the Ordovician. Science, 289: 1920–1921.

78. Richard, F, Millot, S, Gardes, M and Selosse, M-A. 2005. Diversity and structuration by hosts of the below-ground mycorrhizal community in an old-growth Mediterranean forest dominated by Quercus ilex L. New Phytol, 166: 1011–1023.

79. Roy, M, Dubois, MP, Proffit, M, Vincenot, L, Desmarais, E and Selosse, M-A. 2008. Evidence from population genetics that the ectomycorrhizal basidiomycete Laccaria amethystina is an actual multihost symbiont. Mol Ecol, 17: 2825–2838.

80. Roy, M, Watthana, S, Stier, A, Richard, F, Vessabutr, S and Selosse, M-A. 2009. Two mycoheterotrophic orchids from Thailand tropical dipterocarpacean forests associate with a broad diversity of ectomycorrhizal fungi. BMC Biol, 7: 51

81. Royal Botanic Gardens, Kew. 2009. World checklist of selected plant families. Available: http://apps.kew.org/wcsp/prepareChecklist.do?checklist = selected_families%40%40259160920/00929686 (http://apps.kew.org/wcsp/preparechecklist.do?checklist=selected_families%40%40259160920/00929686)

82. Saari, SK, Russell, J, Campbell, CD, Alexander, IJ and Anderson, IC. 2005. Pine microsatellite markers allow roots and ectomycorrhizas to be linked to individual trees. New Phytol, 165: 295–304.

83. Sarrocco, S, Matarese, F, Somma, S, Rossi, F, Moretti, A and Vannacci, G. 2011. Biocontrol of Fusarium head blight (FHB) in a multitrophic perspective. IOCB/WPRS Bull, 71: 123–127.

84. Sarrocco, S, Matarese, F, Moretti, A, Haidukowski, M and Vannacci, G. 2012a. DON on wheat crop residues: Effects on mycobiota as a source of potential antagonists of Fusarium culmorum. Phytopathol Mediterr, 51: 225–235.

85. Sarrocco, S, Moncini, L, Pachetti, G, Moretti, A, Ritieni, A and Vannacci, G. in press. Biological control of Fusarium head blight under field conditions. IOCB/WPRS Bull

86. Schüßler, A, Schwarzott, D and Walker, C. 2001. A new fungal phylum, the Glomeromycota: Phylogeny and evolution. Mycol Res, 105: 1413–1421.

87. Selosse, M-A, Weiß, M, Jany, J-L and Tillier, A. 2002. Communities and populations of sebacinoid basidiomycetes associated with the achlorophyllous orchid Neottia nidus-avis (L.) L.C.M. Rich and neighbouring tree ectomycorrhizae. Mol Ecol, 11: 1831–1844.

88. Selosse, M-A, Faccio, A, Scappaticci, P and Bonfante, P. 2004. Chlorophyllous and achlorophyllous specimens of Epipactis microphylla (Neottieae, Orchidaceae) are associated with ectomycorrhizal septomycetes, including truffles. Microbiol Ecol, 47: 416–426.

89. Selosse, M-A, Richard, F, He, X and Simard, S. 2006. Mycorrhizal networks: Les liaisons dangereuses. Trends Ecol Evol, 11: 621–628.

90. Selosse, M-A, Setaro, S, Glatard, F, Richard, F, Urcelay, C and Weiß, M. 2007. Sebacinales are common mycorrhizal associates of Ericaceae. New Phytol, 174: 864–878.

91. Selosse, M-A and Rousset, F. 2011. The plant-fungal marketplace. Science, 333: 828–829.

92. Shefferson, RP, Kull, T and Tali, K. 2008. Mycorrhizal interaction of orchids colonizing Estonian mine tailings hills. Am J Bot, 95: 156–164.

93. Shefferson, RP, Weiss, M, Kull, T and Taylor, DL. 2005. High specificity generally characterizes mycorrhizal association in rare lady's slipper orchids, genus Cypripedium. Mol Ecol, 14: 613–626.

94. Shendure, J and Ji, H. 2008. Next-generation DNA sequencing. Nat Biotechnol, 26: 1135–1145.

95. Simard, SW, Beiler, KJ, Bingham, MA, Deslippe, JR, Philip, LJ and Teste, FP. 2012. Mycorrhizal networks: Mechanisms, ecology and modelling. Fungal Biol Rev, 26: 39–60.

96. Smith, ME, Douhan, G, Fremier, AK and Rizzo, DM. 2009. Are true multihost fungi the exception or the rule? Dominant ectomycorrhizal fungi on Pinus sabiniana differ from those on co-occurring Quercus species. New Phytol, 182: 295–299.

97. Smith, SE. 1967. Carbohydrate translocation in orchid mycorrhizas. New Phytol, 66: 371–378.

98. Smith, SE and Read, DJ. 2008. Mycorrhizal symbiosis, 3rd ed, San Diego, CA: Academic Press.

99. Song, YY, Zeng, RS, Xu, JF, Li, J, Shen, X and Yihdego, WG. 2010. Interplant communication of tomato plants through underground common mycorrhizal networks. PLoS ONE, 5: e13324

100. Straker, CJ. 1996. Ericoid mycorrhiza: Ecological and host specificity. Mycorrhiza, 6: 215–225.

101. Suárez, JP, Weiss, M, Abele, A, Garnica, S, Oberwinkler, F and Kottke, I. 2006. Diverse tulasnelloid fungi form mycorrhizas with epiphytic orchids in an andean cloud forest. Mycol Res, 110: 1257–1270.

102. Taylor, DL and Bruns, TD. 1999. Population, habitat and genetic correlates of mycorrhizal specialization in the cheating orchids Corallorhiza maculata and C. mertensiana. Mol Ecol, 8: 1719–1732.

103. Taylor, DL, Bruns, TD, Leake, JR and Read, DJ. 2002. “Mycorrhizal specificity and function in myco-heterotrophic plants”. In The ecology of mycorrhizas. Ecological Studies, Edited by: van der Heijden, MGA and Sanders, IR. Vol. 157, 375–414. Berlin: Springer Verlag.

104. Taylor, DL and McCormick, MK. 2008. Internal transcribed spacer primers and sequences for improved characterization of basidiomycetous orchid mycorrhizas. New Phytol, 177: 1020–1033.

105. Tedersoo, L, Pellet, P, Koljalg, U and Selosse, M-A. 2007. Parallel evolutionary paths to mycoheterotrophy in understorey Ericaceae and Orchidaceae: Ecological evidence for mixotrophy in Pyroleae. Oecologia, 151: 206–217.

106. Tisserant, E, Kohler, A, Dozolme-Seddas, P, Balestrini, R, Benabdellah, KColard, A. 2012. The transcriptome of the arbuscular mycorrhizal fungus Glomus intraradices (DAOM 197198) reveals functional tradeoffs in an obligate symbiont. New Phytol, 193: 755–769.

107. Torta, L, Leone, V, Caldarella, CG, Lo Verde, G, Burruano, SVitale, A. 2008. Microrganismi fungini associati al Punteruolo Rosso delle palme in Sicilia. Report – Regione Sicilia, Assessorato Agricoltura e Foreste Progetti FITOPALMINTRO- MEDEA, 1: 52–57.

108. van der Heijden, MGA, Klironomos, JN, Ursic, M, Moutoglis, P, Streitwolf-Engel, RBoller, T. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature, 396: 72–75.

109. van der Heijden, MGA, Wiemken, A and Sanders, IR. 2003. Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plants. New Phytol, 157: 569–578.

110. van der Heijden, MGA, Scheublin, TR and Brader, A. 2004. Taxonomic and functional diversity in arbuscular mycorrhizal fungi – Is there any relationship?. New Phytol, 164: 201–204.

111. Vandenkoornhuyse, P, Ridgway, KP, Watson, IJ, Fitter, AH and Young, JPW. 2003. Co-existing grass species have distinctive arbuscular mycorrhizal communities. Mol Ecol, 12: 3085–3095.

112. van der Putten, WH. 1997. Die-back of Phragmites australis in European wetlands: An overview of the European Research Programme on reed die-back and progression (1993–1994). Aquat Bot, 59: 263–275.

113. Vega, FE, Goettel, MS, Blackwell, M, Chandler, D, Jackson, MAKeller, S. 2009. Fungal entomopathogens: New insights on their ecology. Fungal Ecol, 2: 149–159

114. Venturella, G, Altobelli, E, Bernicchia, A, Di Piazza, S, Donnini, DGargano. 2011. Fungal biodiversity and in situ conservation in Italy. Plant Biosyst, 145: 950–957.

115. Vitale, A, Leone, V, Torta, L, Burruano, S and Polizzi, G. 2008. Prove preliminari di lotta biologica con Beauveria bassiana e Metarhizium anisopliae nei confronti del Punteruolo rosso. La ricerca scientifica sul punteruolo rosso e gli altri fitofagi delle palme in Sicilia. Report – Regione Sicilia, Assessorato Agricoltura e Foreste Progetti FITOPALMINTRO- MEDEA, 1: 169–172.

116. Vrålstad, T, Myhre, E and Schumacher, T. 2002. Molecular diversity and phylogenetic affinities of symbiotic root-associated ascomycetes of the Helotiales in burnt and metal polluted habitats. New Phytol, 155: 131–148.

117. Windels, C. 2000. Economic and social impacts of Fusarium head blight: Changing farms and rural communities in the northern great plains. Phytopathology, 90: 17–21.

118. Wright, MM, Cross, R, Cousens, RD, May, TW and McLean, C. 2010. Taxonomic and functional characterisation of fungi from the Sebacina vermifera complex from common and rare orchids in the genus Caladenia. Mycorrhiza, 20: 375–390.

119. Xu, X and Nicholson, P. 2009. Community ecology of fungal pathogens causing wheat head blight. Ann Rev Phytopathol, 47: 83–103.

120. Zampieri, E, Murat, C, Cagnasso, M, Bonfante, P and Mello, A. 2010. Soil analysis reveals the presence of an extended mycelial network in a Tuber magnatum truffle-ground. FEMS Microbiol Ecol, 71: 43–49.